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The Sheep Project (2): The effects of plane of nutrition, castration and the timing of first breeding in ewes on dental eruption and wear in unimproved Shetland sheep

Fay Worley *, Polydora Baker, Peter Popkin [1], Andy Hammon, Sebastian Payne [2]

Historic England (formally English Heritage), Fort Cumberland, Eastney, Portsmouth PO4 9DL, UK

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ABSTRACT

The skeletons of 356 unimproved Shetland sheep from flocks kept at two nutritional levels are used to investigate the effects of nutritional level on the timing of mandibular dental eruption, and of wear in the mandibular fourth premolar and molars; comparisons are also made between entire and early-castrated males and between unbred, early-bred and late-bred ewes. Sheep weights and counts of permanent anterior teeth recorded during life are also investigated. The skeletal dental data are compared to timing of bone fusion recorded for the same individuals (Popkin et al., 2012).

Results show small differences in the timing of eruption and tooth wear between males and females, and that these processes are only marginally affected by castration and the timing of first breeding in ewes. Small differences between sheep at the two nutritional levels are also present; however the difference between the two feeding regimes was moderate, and more marked nutritional differences might have larger effects.

The implication of our data is that marked intra-assemblage differences cannot be explained exclusively by changes in the management variables explored in this study. Further, as sex and castration have little effect on the timing of dental eruption and wear, but substantially delay epiphyseal fusion (Popkin et al., 2012), we support previous hypotheses that comparison of the two datasets may provide a method for investigating flock structure in past animal husbandry. Our results are of most relevance to domestic sheep assemblages from similar environments to the UK, and to the Shetland breed, but can assist zooarchaeologists worldwide in interpreting dental data.

1. Introduction

The sheep project was set up to investigate the effect of nutrition, sex, castration and pregnancy on skeletal development, in order to inform and improve zooarchaeological interpretations of sheep husbandry. These themes are explored in our previous publication (Popkin et al., 2012), which focused on their significance to bone maturation and post-cranial biometry, and demonstrated clear influences of sex, castration and nutrition in the timing of bone fusion. Osteological implications of breeding age in ewes were also considered by Baker et al. (2014).

This paper presents data for the timing of tooth eruption and rate of tooth wear, and their relationship with nutrition, sex, castration and pregnancy, within a flock of 356 domestic sheep (*Ovis aries*) of known life history with age at death resolved to the day. Impact of sex and management is discussed in relation to individual teeth; age estimation, including derived mandible wear stages, is not considered. The flock comprises unimproved Shetland sheep, raised outdoors in Scotland. The data are of direct relevance to similar environmental conditions and breeds, but can also contribute to understanding domestic sheep assemblages elsewhere.

1.1. Tooth eruption and wear: factors influencing sequence and timing

Sheep teeth erupt, wear down and are replaced in a known sequence. The progression of this sequence, particularly in anterior teeth, is traditionally used to age and assess the quality of farm stock, and has therefore been commonly recorded in live animals (for example, Botkin et al., 1988, 8–9; Brown, 1913, 45–51; McGregor, 2011; Simonds, 1854). The sequence of eruption is consistent between domestic sheep breeds, and varies only slightly between domestic sheep and goats (*Capra hircus*) (Jones, 2006). Inconsistencies between wild sheep species, for example *Ovis dalli* and *Ovis canadensis* (Hemming, 1969), are not relevant to British assemblages, which comprise only domestic sheep and goats.

The timing of sheep tooth eruption differs between breeds (e.g., for anterior teeth see Aitken and Meyer, 1982; Arrowsmith et al., 1974; Wiener and Purser, 1957) and sexes (Section 2.1.1), reflecting their different rates of maturation, and is associated with weight gain

* Corresponding author.
E-mail address: fay.worley@HistoricEngland.org.uk (F. Worley).
[1] Current affiliation: Golder Associates.
[2] Current affiliation: Independent.

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(McGregor, 2011). The timing of eruption is also suggested to vary in sheep subject to differing environmental factors, for example nutrition (Section 2.2.1) and stocking levels. Tooth wear is the progressive attrition of enamel. Its rate reflects the time that the tooth has been in occlusion (and therefore any influences on timing of eruption) together with the morphology and robusticity of the tooth enamel in question (both of which may reflect genetic and environmental variation), the abrasiveness of ingested food and contaminants (including seasonal variations), and time spent eating, ruminating or tooth grinding (Every et al., 1998). Eating behaviours may themselves be influenced by the sexes differing nutritional requirements for growth and reproduction, food availability (Galvani et al., 2010), forage preference (sheep are selective grazers; Guðmundsson and Dýmundsson, 1989) including influence of territorial and social behaviour (Dumont and Boissy, 2000), stocking levels (Guðmundsson, 1993), and even weather conditions (for example temperature, Kennedy, 1983).

Since the 1960s, zooarchaeology has increasingly investigated the sequence of dental eruption and wear in archaeological sheep mandibles. Several methods for categorising the progressive eruption of teeth and exposure of dentine have been published (for example, Ewbank et al., 1964; Grant, 1975; Grant, 1982; Payne, 1973; Payne, 1987). More recently, research has begun to investigate the relationship between dental succession, age, sex, breed, castration and nutrition, using modern collections of sheep (Clutton-Brock et al., 1990; Greenfield and Arnold, 2008; Hatting, 1983; Jones, 2006; McGregor, 2011; Moran and O'Connor, 1994; Zeder, 2006).

1.2. Zooarchaeological research potential

Zooarchaeological interpretation is often comparative, investigating evidence for social, cultural, chronological or spatial similarity and difference in husbandry and animal utilisation. Sheep dental data is used to estimate age at death and suggest flock structures and product utilisation, quality of meat consumed, and seasonality of slaughter whether for everyday or festive/ceremonial activities. The validity of intra- or inter-site comparison often relies on assumed minimal influence of forage quality (associated with status, geography and topography) and management practices (including castration and breeding of ewes) on dental data. However, these factors do influence post-cranial skeletal development (growth and fusion) in the population under study (Popkin et al., 2012).

The known life history dental data presented here therefore offer two primary opportunities. Firstly, to refine and clarify understanding of the influence of forage quality and flock management on dental eruption and tooth wear, and secondly to investigate whether any differences seen in dental processes can be compared to variation in epiphyseal fusion, in order to investigate sheep management practices for comingled assemblages, or to confirm sex in articulated skeletons. The implications of our data on age at death estimation are considered elsewhere (Worley et al., in preparation).

2. Background

This section reviews previous research into the impact of sex and nutrition on tooth development and wear. It also summarises previous research into how sex and nutrition affected other maturation and growth characteristics of the study population (i.e., osteometric and bone fusion data).

2.1. Impact of breed, sex and management (castration of rams, breeding age in ewes) on sheep

2.1.1. Comparative research on tooth eruption and wear with reference to breed, sex and management

In a precursor to this research, Moran and O'Connor (1994) noted that there are few reliable data regarding differences in tooth eruption. The majority of research has focussed on incisor eruption. Comparing males and ewes, some sources suggest male first incisors erupt slightly earlier (Field et al., 1990; Simonds, 1854, 87), while others found little or no difference (Ho et al., 1989), even in large samples (Matika et al., 1992). Castration has been reported to result in earlier eruption by some authors (Clutton-Brock et al., 1990 incisor and cheek tooth data, Ho et al., 1989 incisor data for Finn x Whiteface), while others have found little effect (for example Davis, 2000 cheek tooth data, Hatting, 1983 incisor data), although some wethers exhibited advanced eruption in Hatting's small dataset. Differences in eruption between rams, wethers and ewes are also impacted by breed (as shown in Ho et al., 1989).

We are not aware of studies on tooth eruption in relation to age at first mating in ewes. It is possible that breeding ewe lambs (under 12 months) impacts on tooth eruption through reduced live weight (McGregor, 2011, 81; see Kenyon et al., 2011, 327 for live weight studies), though a direct effect of early breeding on eruption has not been reported. Studies of breeding age and tooth wear have indicated that ewes successfully bred when young (<12 months) may suffer a greater incidence of broken mouth, and incisor wear and loss when adult (6 years and older), which can impact on their condition and productivity (McGregor, 2011, 82, 83).

There are few studies of the effect of sex on tooth wear. Davis found slight accelerated wear in Shetland rams relative to wethers (Davis, 2000), but Jones (2006) found no difference between ewes and rams for some mandible wear stages in 3 to 8 month old animals. She considered her dataset for older sheep too small to draw useful conclusions, although her data show slight advanced median mandible wear stage for ewes at 13 months (Jones, 2006, Fig. 14).

2.1.2. Previous results of sex, castration and breeding impacts on other maturation and growth characteristics of the subject population

2.1.2.1. Sex, castration, breeding and growth (osteometric data). Popkin et al. (2012) demonstrated that bone growth is not uniform across the skeleton, but varies by element portion and by plane of growth depending on the sex and castration status of the individual. In general terms, sex has the strongest influence on bone growth with ewes being smaller than both rams and wethers. Wether elements are always longer than ewe elements but wether femur, humerus, astragalus and calcaneus are not always longer than the ram counterparts. Differences in bone growth between the sexes also vary by plane of nutrition, as described below. Breeding and early breeding limit the potential for skeletal growth (size, shape, variability) in ewes (Baker et al., 2014).

2.1.2.2. Sex, castration, breeding and skeletal maturity (bone fusion data). Popkin et al. (2012) demonstrated that both sex and nutrition significantly affect the timing of fusion in post-cranial skeletal elements. In later fusing elements, castration leads to a delay in epiphyseal fusion of up to 12 months relative to rams and up to 21 months relative to ewes. Ewes consistently show the earliest onset and completion of fusion relative to both wethers and rams. Early breeding impacts completion of fusion in ewes, which may be due to slowing of the fusion process or, in some cases, to a delay in the onset of fusion (Baker et al., 2014).

2.2. Impact of nutrition on sheep

2.2.1. Comparative research on tooth eruption and wear with reference to nutrition

Moran and O'Connor's (1994) research noted a general dearth in data on the impact of nutrition on dental development, citing Tschirvinsky (1909), Franklin (1950) and a series of papers published in the 1960s (Cutress and Healy, 1965; Healy et al., 1967; Healy and Ludwig, 1965) as exceptions. Research into the impact of nutritional mineral and vitamin deficits (for example, Franklin, 1950; see also

McGregor, 2011, 82) are not considered here. The available research has primarily been undertaken within agricultural science rather than zooarchaeology, its focus therefore tending to favour incisor eruption and attrition rather than the cheek tooth row. Several authors report that improved nutrition can accelerate incisor eruption. Wiener and Purser (1957) found earlier incisor eruption associated with provision of feed supplements and lower stocking levels, while Purser et al. (1982) and Gunn (1967) note accelerated incisor eruption with improved nutrition, achieved by bringing sheep down from hill pasture to lower ground or indoor conditions over winter. Arrowsmith et al. (1974), similarly found that incisor eruption is expedited by supplemental feeding. Field et al. (1990) noted no difference in incisor eruption in wethers and ewes between high and low energy corn silage diets, however their data show that within the ewe dataset eruption is delayed in the low nutrition group. Tschirvinsky (1909) found nutrition to have a lesser impact on eruption than on bone fusion.

McGregor (2011) relates incisor eruption to both live weight and seasonal live weight gain, in addition to sex, and reports research findings where eruption was concentrated in summer months (citing Barnicoat, 1957). We are not aware of any studies on the effect of nutrition on tooth eruption in ewes bred at different ages. However, nutrition does impact on young bred ewe live- and fleece-weights, and lamb weight and survival, though there may not be a lasting effect as the ewes age (Kenyon et al., 2011; McCall and K, 1981; McGregor, 2011; Salisbury et al., 2000).

The impact of feeding on tooth wear has been long recognised, although we are not aware of any experimental studies on cheek tooth wear and nutrition. Simonds (1854, 83) noted that the condition of teeth (degree of wear) will depend on management and food, noting increased wear in 'heathland' sheep. Later experimental research concluded that soil ingestion is a major cause of incisor tooth wear, and can vary with annual cycles of plant growth (Healy et al., 1967; Healy and Ludwig, 1965; Ludwig et al., 1966), and with stocking level (Arnold and Bush, 1962; McGregor, 2011). Healy and Ludwig (1965) also comment on the role of plant ecology in sheep tooth wear, both through abrasiveness of species (e.g., phytoliths) and their capacity to facilitate or reduce soil exposure and ingestion.

Every et al. (1998) investigate the mastication mechanism in sheep, noting the nature of abrasive wear from chewing (both eating and ruminating) on both anterior and cheek teeth. Behavioural differences in chewing and ruminating are seen when sheep are subject to food restrictions (Galvani et al., 2010).

2.2.2. Previous results of impact of nutrition on the subject population

2.2.2.1. Nutrition and growth (osteometric data). Popkin et al. (2012) demonstrated that the plane of nutrition influences bone growth in a complex fashion depending on the sex and castration status of the animal as well as on the element and plane of growth considered. High nutrition ewes consistently have longer limb bones than low nutrition ewes. Low nutrition affects growth in unbred and breeding ewes, and impacts early bred ewes in particular (Baker et al., 2014). Nutrition has no measurable effect on wether limb bone length and only affects radius and tibia length in rams (being longer with high nutrition). Other measurement planes show complex interplay between sex and nutrition. For example, the size of the tibia Bd (von den Driesch, 1976) is significantly affected by nutrition in all sexes, and by castration except in low nutrition animals, while femur Bd is not significantly affected by nutrition in any sex but is always significantly affected by castration.

2.2.2.2. Nutrition and skeletal maturity (bone fusion data). Popkin et al. (2012) demonstrated that the plane of nutrition influences both the timing and duration of the fusion process. Low nutrition animals experience a broader range of fusion timing than high nutrition animals. With one or two minor exceptions, rams, ewes and wethers raised on the high plane of nutrition consistently showed advanced fusion compared to those raised on the low plane of nutrition. This pattern is also seen in early bred and unbred ewes, but not late bred ewes (Baker et al., 2014).

3. Material and methods

3.1. Sheep studied

The subject flock was raised under experimental conditions from birth and contained 356 unimproved Shetland sheep. Relevant parameters of husbandry (nutrition, age of castration and breeding, and age at death) are presented here; further information is provided in Popkin et al. (2012). Weight and anterior tooth presence were recorded throughout life (live data), and anterior and cheek tooth eruption and wear were observed from prepared skeletons (skeletal data) as described below (Section 3.2).

Table 1
Live weigh-in/tooth count dates, with sample size and age ranges for weigh-in data.

Nominal age (months)	Cohorts observed	Date of observation		n	Min age		Max age	Max age	Range
		Month	Day/year		(Days)	(Months)	(Days)	(Months)	(Days)
3	1–9	August	08/96; 04/97; 10/98; 09/99; 22/00; 08/01	356	59	1.9	105	3.5	46
6	1–9	November	06/96; 04/97; 03/98; 06/99; 13/00; 14/01	356	151	5.0	194	6.4	43
9	2–9	February	05/97; 28 [Jan]/98; 02/99; 03/00; 08/01	308	236	7.8	285	9.4	49
12	2–9	May	07/97; 05/98; 05/99; 05/00; 18/01	308	333	10.9	376	12.4	43
15	2–9	August	04/97; 10/98; 09/99; 22/00; 08/01	308	430	14.1	477	15.7	47
18	3–9	November	04/97; 03/98; 06/99; 13/00; 14/01	284	515	16.9	560	18.4	45
21	4–9	February	28 [Jan]/98; 02/99; 03/00; 08/01	260	606	19.9	647	21.3	41
24	4–9	May	05/98; 05/99; 05/00; 18/01	260	698	22.9	746	24.5	48
27	4–9	August	10/98; 09/99; 22/00; 08/01	260	794	26.1	847	27.8	53
30	5–9	November	03/98; 06/99; 13/00; 14/01	228	883	29.0	930	30.6	47
33	6–9	February	02/99; 03/00; 08/01	180	972	32.0	1017	33.4	45
36	6–9	May	05/99; 05/00; 18/01	180	1064	35.0	1116	36.7	52
39	6–9	August	09/99; 22/00; 08/01	180	1166	38.3	1210	39.8	44
42	7–9	November	06/99; 13/00; 14/01	140	1255	41.3	1295	42.6	40
45	8–9	February	03/00; 08/01	80	1343	44.1	1380	45.4	37
48	8–9	May	05/00; 18/01	80	1436	47.2	1479	48.6	43
51	8–9	August	22/00; 08/01	80	1524	50.1	1579	51.9	55
54	9	November	13/00; 14/01	40	1628	53.5	1662	54.6	34

3.1.1. Feeding regimes, environment, climate

The sheep were bred and raised outdoors within the Pentland Hills Regional Park at the Scottish Agricultural College (SAC; now part of Scotland's Rural College), Midlothian, Scotland, between 1996 and 2001. The SAC estate sits on a mixture of clayey loam to sandy loam and sand to sandy loam (UKSO, 2015; contains British Geological Survey materials (c) NERC [2015]) at an altitude of 200 m. We do not have weather data for the site, however local average daily temperatures (1981–2010, recorded approximately 15 km to the north), range from 11 to 19 °C in the hottest summer months and 1 to 7 °C in the coldest winter months (The Royal Botanic Garden Edinburgh, 2015). Between 1976 and 2010 the area experienced an annual average of 215 days with rain, 9 days with snow, and 131 days with grass frost (The Royal Botanic Garden Edinburgh, 2011). The annual averages for grass frost frequency differed by up to 18 days over the period the sheep were raised.

The sheep were divided into two flocks of equal composition and raised in fields that provided forage of differing nutritional quality to produce a high plane and a low plane flock. The low plane flock was primarily pastured on poorly drained native grassland, while the high plane flock was primarily held in an adjacent field of improved grassland, undersown with barley and reseeded with 36 kg/ha of a perennial ryegrass and white clover mix in April 1994 (Dingwall et al., 1996).

The feeding regimes were designed to be analogous to those of well- and poorly-fed medieval flocks in the UK, whilst adhering to late 20th century welfare considerations. Both flocks were therefore given supplementary hay during periods of snow cover and the low plane sheep were moved to a different field if SAC considered their weight loss to be unacceptable. No ecological survey of the fields was conducted and feeding behaviors (including any preference for particular forage within the fields) were not recorded. No concentrate feed was provided. In this paper, live weight is investigated as a comparative measure of the impact of the two nutritional regimes.

3.1.2. Flock breakdown and husbandry: castration and breeding

Each flock included rams, wethers (castrated at a few days old) and ewes. Here, 'males' is used to indicate entire and castrated rams. The ewes either remained unbred, were early bred or late bred the latter groups lambing annually from either two or three years.

The sheep were slaughtered in nine age groups (cohorts 1 to 9, aged approximately 7, 16, 19, 28, 31, 40, 43, 52 and 55 months; see Popkin et al., 2012) with their age at death known to the day. Sheep were slaughtered twice a year. Slaughter dates avoided periods of gestation, lambing and nursing, resulting in age cohorts separated by nine and three months alternately. Variation in date of birth leads to variation in age at death of 29 to 54 days in each cohort if all sheep are combined, but predominantly restricted to 14–35 days within sex-plane-age cohorts (Popkin et al., 2012, 1777). The sheep were not raised contemporaneously, but included animals born into the flock over several years, from 1996 to 2001. The youngest age cohort includes some animals from the second generation of the flock. The number of sheep in each cohort varies, but is always consistent between the high and low plane flocks, and always includes at least four individuals in each sex-husbandry group.

3.2. Recording methods and conventions

3.2.1. Live weight data

The sheep were weighed at birth and then tri-monthly throughout their lives. All sheep were weighed over one or two days each February, May, August and November. At each weigh-in, sheep varied in age, with a range of up to 55 days, due to variation in date of birth and varying observation dates over multiple years (Table 1). No bias towards any sex or nutrition group is evident in absolute ages at observation (supplementary data Fig. A1). May weigh-ins occurred while some ewes were pregnant and others had given birth. May weigh-in data are therefore excluded from the early and late bred ewe groups (i.e., 12, 24, 36, 48 months, as appropriate).

3.2.2. Live eruption data

A count of the total number of permanent anterior teeth (incisors and canines) that had erupted through the gum was observed and recorded at each weigh-in from the age of nine months. There is some variation in the age of individual sheep at weigh-in (see Section 3.2.1). The position of the erupted teeth was not noted. Here we assume sequential eruption, supported by our skeletal data, and bilateral symmetry, i.e., a count of three implies left and right first incisors and a single second incisor.

3.2.3. Skeletal eruption and wear data

Left permanent mandibular teeth were recorded with the teeth from the right side substituted where the left was lost or broken (i.e., crown damaged preventing accurate allocation to wear stage).

Anterior teeth were recorded as erupted and unworn (U), in wear (W), or broken (B). The position was scored as d&U if both the erupted permanent tooth and its deciduous predecessor were present.

Cheek tooth eruption (of fourth deciduous premolar, dp4; fourth premolar, P4; first, second and third molars, M1, M2 and M3) was recorded following Ewbank et al. (1964): crypt perforated (C), tooth visible in crypt (V), tooth erupting through bone (E), tooth half erupted (½). Cheek tooth wear was recorded for dp4, P4, M1, M2 and M3 following Payne (1987), with the stage reduced to its numeric prefix for data analysis. Broken tooth crowns were demarked 'B'.

3.3. Exclusion of teeth/individuals

Teeth were excluded from analyses if broken, misshaped through non-metric variation, misaligned in the jaw (impacted), or associated with pathology (abscess or new bone formation) due to the potential impact of altered chewing behaviour or atypical wear. A small number of teeth were recorded as being incompletely erupted, yet in early stages of wear; these are also excluded from the skeletal eruption and wear datasets. Anterior tooth rows were excluded from the live eruption dataset if any tri-monthly observation showed a reduction in the number of teeth since the last observation. Three skeletal ewe anterior tooth rows presented with unworn teeth in two adjacent positions, these were excluded as they could not be securely positioned within the ordinal sequence of eruption and wear.

3.4. Examining variation: statistical methods

Data in this paper are quantified by number of teeth, number of anterior tooth rows, and number of individuals. The sample size for each comparison of the data varies within age–sex–husbandry cohorts. The skeletal tooth eruption and wear data are ordinal and therefore best described by minimum, maximum, median and modal scores. To examine differences in skeletal data from sex and management groups we employ statistical tests of significance; the Kruskal–Wallis test (applied using an online statistical package: http://vassarstats.net/) for three or more independent samples of at least five records, and Mann–Whitney two-tailed tests (Hammer et al., 2001) for two samples. The null hypotheses tested were that the tooth eruption and wear scores of high and low plane sheep, or bred and unbred ewes do not differ within each cohort or cohort pair (Mann–Whitney tests) and that the mean ranks of ram, wether and ewe eruption or wear scores do not substantially differ within cohorts or cohort pairs (Kruskal–Wallis tests). Skeletal eruption codes were converted to a numeric value for statistical tests (anterior teeth values were calculated as a score of two for each permanent tooth in wear, plus one for each unworn permanent tooth present). Statistical test results and sample sizes are given in the supplementary data tables. Raw data for significantly varied groups are presented in figures throughout the text.

Table 2
Dataset for skeletal cheek tooth eruption and wear (number of teeth).

Cohort and age	Tooth	Ram		Wether		Early bred ewe		Late bred ewe		Unbred ewe		All ewes		Total	
	Nutrition	H	L	H	L	H	L	H	L	H	L	H	L	H	L
Eruption dataset															
Cohort 1 (7 months)	M2	8	8	8	8	–	–	–	–	8	8	8	8	24	24
Cohort 2 (16 months)	M3	4	4	4	4	–	–	–	–	4	4	4	4	12	12
Cohort 3 (19 months)	M3	4	4	3	4	–	–	–	–	4	4	4	4	11	12
	P4[a]	2	–	1	–	–	–	–	–	1	–	1	–	4	–
Wear dataset															
Cohort 1 (7 months)	M1	8	8	8	8	–	–	–	–	8	8	8	8	24	24
Cohort 2&3 (16 & 19 months)	dp4/P4	7	7	7	7	–	–	–	–	8	7	8	7	22	21
	M2	8	8	8	8	–	–	–	–	8	8	8	8	24	24
Cohort 4&5 (28 & 31 months)	P4	8	9	10	8	10	9	–	–	10	9	20	18	38	35
	M2	9	9	10	10	10	10	–	–	10	10	20	20	39	39
	M3	9	9	10	10	10	10	–	–	10	8	20	18	39	37
Cohort 6&7 (40 & 43 months)	P4	8	9	7	7	10	8	8	6	9	7	27	21	42	37
	M1	7	9	10	10	10	9	10	10	10	10	30	29	47	48
	M3	8	9	10	10	10	10	9	10	10	10	29	30	47	49
Cohort 8&9 (52 & 55 months)	P4	7	7	8	8	7	7	6	8	7	6	20	21	35	36
	M1	6	7	8	8	8	8	8	7	8	8	24	23	38	38
	M3	7	7	8	8	8	7	8	8	8	8	24	23	39	38

[a] All other sheep in cohort 3 retained the dp4 in wear.

4. Results

4.1. Description of dental data and opportunities for observation of variation

The data show a tooth eruption sequence of dp4/M1 (both already in wear in the youngest sheep), M2, M3, and finally P4, a pattern consistent with previous research (e.g., Jones, 2006). Skeletal data for anterior teeth (incisors and canine) also show an expected sequence of eruption: first, second, third incisors and canines, with the first incisor coming into wear while the M3 is erupting (stages V, E and ½).

The live data provide the finest resolution dataset and largest sample sizes for examining impact of sex and management on the eruption of anterior teeth, but cannot be assumed to show the same impact as the cheek teeth, which are of more relevance to zooarchaeological analysis.

Cheek tooth eruption data were available for M2, M3 and four P4s (Table 2). In isolation, the dataset for P4 eruption is insufficient to examine influence of sex or husbandry; it is integrated into the sequence of dp4 and P4 wear stages in cohort 2&3 for statistical analysis.

Data for cheek tooth wear are available for the dp4/P4, M1, M2 and M3, in all age cohorts following eruption. For analysis, most cohorts were grouped into closely aged pairs (2&3, 4&5, 6&7, and 8&9) due to the similarity of the data within each pair (Worley et al., in preparation). The potential for variation in wear to be evident is impacted by the longevity of individual wear stages, which reflects both rate of attrition and tooth morphology. The enamel structure of sheep molars results in a series of short-lived wear stages in early wear, followed by a persistent stage, and finally a second series of shorter-lived stages (Grant, 1982; Payne, 1973). The shorter lived wear stages provide a more sensitive record with the greatest potential to show variation. Persistent wear stages dominate teeth in several cohorts in our data set, and are represented in all but two molar cohorts (M1 cohort 1, M3 cohort 4&5). The timing of tooth eruption together with the dominance of long-standing wear stages within the dataset restricts examination of variation to those teeth and cohorts listed in Table 2.

4.2. Impact of nutrition

4.2.1. Nutrition and live weight

The nutritional regimes were sufficiently different to impact on growth. From six months old, low plane sheep weighed around 10% less than high plane sheep, with a difference in mean weight between the two flocks of up to 6 kg (Fig. 1). Low plane sheep were also lighter than high plane sheep within each sex group. The impact of nutrition is particularly evident on the early bred ewes, before first lambing and on their subsequent growth (as described by Baker et al., 2014).

Annual cycles of weight gain and loss can be seen in the high and low flocks with weight loss usually seen between the November and February weigh-ins (observations at 6–9, 18–21, 30–33, 42–45 months), often preceded by an autumn slowing of weight gain (Fig. 1).

4.2.2. Nutrition and anterior tooth eruption

Considering all sexes and breeding groups combined, live data show considerable overlap in the ranges for each nutrition group, but with very slight advanced average (mean) eruption of all incisors (i.e., up to the sixth tooth in Fig. 2A) in high plane sheep, and the reverse seen in canines. This pattern is heavily influenced by that seen in ewes, due to differences in sample size between sexes (Fig. 2C). If the median number of tooth pairs erupted is considered, the high plane sheep reach four-, six- and eight-tooth state one observation earlier than the low plane sheep, with no difference in the first incisors. The live data show a slight acceleration in the rate of anterior tooth eruption over the summer months, which corresponds to periods of increasing weight (Fig. 2B, see Section 4.2.1).

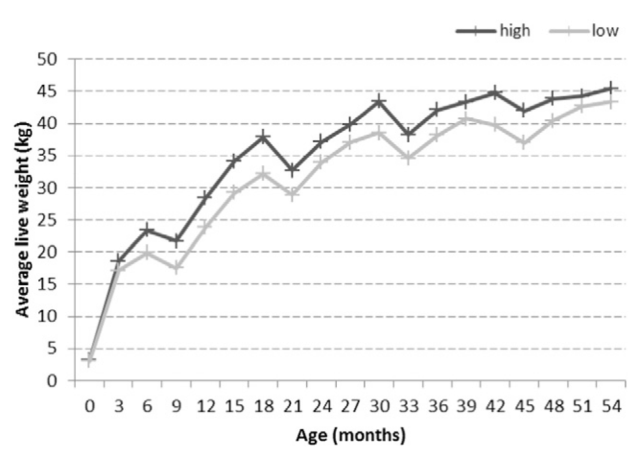

Fig. 1. Live weight data for high and low nutrition flocks (mean values), see Table 1 for sample size.

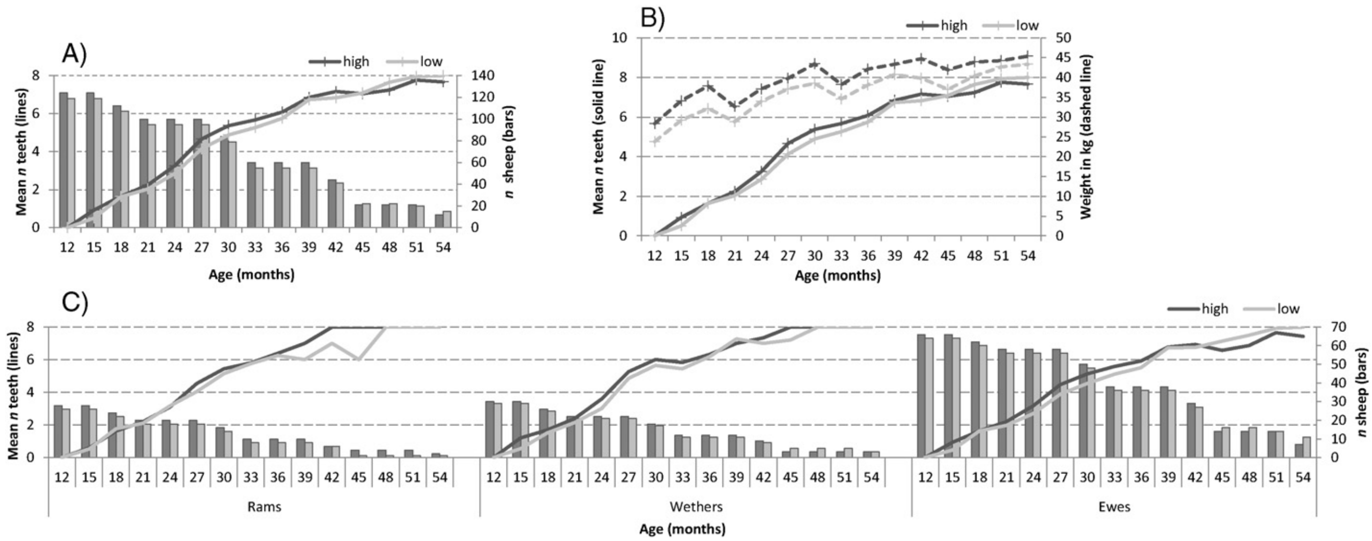

Fig. 2. Live data for permanent incisor and canine presence in high and low plane flocks. A) All sheep, tooth presence and sample size; B) all sheep, tooth presence and live weight; C) tooth presence and sample size for rams, wethers and ewes.

Skeletal data offer additional evidence that low quality nutrition can retard anterior tooth eruption. Median anterior tooth eruption is slightly advanced in high plane sheep in cohort 5 when sexes are combined and in cohorts 5 and 7 when ewes are considered separately (Fig. 3); only the variation in these cohorts is statistically significant (supplementary data Table A1).

4.2.3. Nutrition and cheek tooth eruption and wear

Considering the cheek tooth row used for zooarchaeological age at death estimation, skeletal data show that the timing of M2 and M3 eruption are very similar in sheep raised on low and high plane nutrition, both when sexes are combined and within each sex group (supplementary data Table A2). No variation is statistically significant.

While the difference in nutrition does not impact M2 and M3 eruption, it does impact tooth wear, with some statistically significant differences (Table 3, supplementary data Table A2), although in all tooth-cohorts data overlap. Examining the data irrespective of sex or breeding status, the M3 in cohort 4&5 shows significant differences between the high and low flock. Significant variation persists within some sex and breeding groups in this tooth-cohort, and is also seen in the P4 in cohort 4&5 and the M1 in cohort 6&7 in some groups. Ram wear is not significantly affected by low nutrition in our dataset, while wether, and more frequently ewe wear are impacted. While the Mann–Whitney test does not identify the direction of any variation, the median values for each significant result suggest that the low nutrition regime usually resulted in reduced tooth wear (Fig. 4, supplementary data Table A2).

Table 3
Summary of Mann–Whitney U test significant differences (p values) in wear between nutritional planes irrespective of and within sex and breeding groups. Full results in supplementary data Table A2.

Tooth	Cohort	Flock	Rams	Wethers	All ewes	Unbred ewes	Early bred ewes	Late bred ewes
M1	1	–	–	–	–	–	n/a	n/a
dp4	2&3	–	–	–	–	–	n/a	n/a
M2	2&3	–	–	–	–	–	n/a	n/a
P4	4&5	–	–	0.036	–	–	0.039	n/a
M2	4&5	–	–	–	–	–	–	n/a
M3	4&5	0.019	–	–	0.005	–	0.026	n/a
P4	6&7	–	–	–	–	–	–	–
M1	6&7	–	–	–	–	0.033	–	–
M3	6&7	–	–	–	–	–	–	–
P4	8&9	–	–	–	–	–	–	–
M1	8&9	–	–	–	–	–	–	–
M3	8&9	–	–	–	–	–	–	–

The P4 and M3 groups exhibiting impact of nutrition are in the youngest post-eruption cohorts and significant differences are observed as

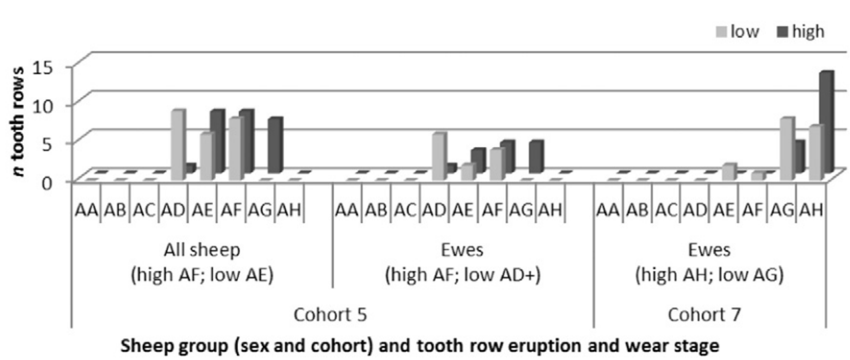

Fig. 3. Skeletal anterior tooth row eruption and wear data, for cohorts showing significant variation by nutrition. Median values in brackets; '+' denotes median value is between the stated and the following stage. Anterior row stages (defined as condition of latest erupting tooth): AA — 1st incisor unworn; AB — 1st incisor worn; AC — 2nd incisor unworn; AD — 2nd incisor worn; AE — 3rd incisor unworn; AF — 3rd incisor worn; AG — canine unworn; AH — canine worn.

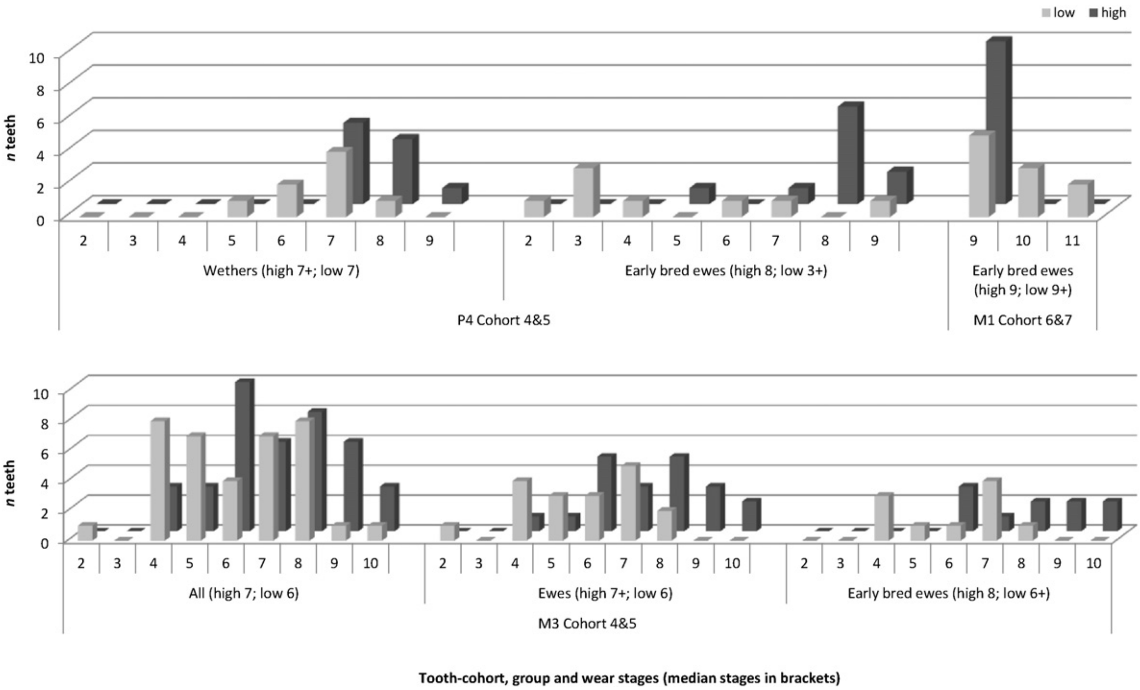

Fig. 4. Cheek tooth eruption and wear data for cohorts showing significant variation by nutrition.

wear progresses through short lived wear stages. In contrast, no significant differences are seen as the M2 passes through short-lived, earliest wear stages in cohort 2&3.

The significant M1 wear scores in cohort 6&7 are influenced by some ewes progressing beyond the longstanding wear stage. No M2s or M3s have worn beyond the longstanding stages 9 and 11 in our dataset.

4.3. Impact of sex and management (castration and breeding age)

4.3.1. Live weight, sex, castration and breeding

Sheep mean live weights vary only slightly with sex at birth, with ewe lambs weighing 3.0 kg, and males 3.2 kg. By the three month weigh-in the ewe, wether and ram lamb weights diverge further, with male growth increasing more rapidly than ewes, which consistently have the lightest mean weight (Fig. 5, see also supplementary data Figure A1). Early breeding results in lighter ewe weight following first lambing compared to late- and unbred ewes (Baker et al., 2014).

These data combine live weights from all sheep irrespective of year of birth, thus averaging any variation seen in individual calendar years. The annual cycles of weight gain and loss can be seen in all sexes, but are least evident in ewes once they approach adult carcass weight.

4.3.2. Sex and management and anterior tooth eruption

Live data average (mean) tooth counts show no difference in the timing of first incisor eruption between sexes (Fig. 6A). Although their data ranges continue to overlap, the remaining anterior teeth show eruption to be advanced in males relative to ewes. The difference is most marked in canines, and particularly in the high plane flock. However, relative eruption rate (mean number of teeth) becomes erratic in low plane rams from the 39 month observation. This may be a reflection of the small dataset with only one low ram observed from 45 months.

Observations of median eruption of each anterior tooth pair tend to coincide with peaks in live weight in males (Fig. 6B), see Section 4.3.1. Median values show no difference in the timing of first incisor eruption between ewes and males, or second incisor eruption between ewes and rams. The data show third incisors and canines erupting earlier in males than ewes. Castration may slightly accelerate second incisor eruption; wether second incisors and canines are erupted one observation earlier than entire rams.

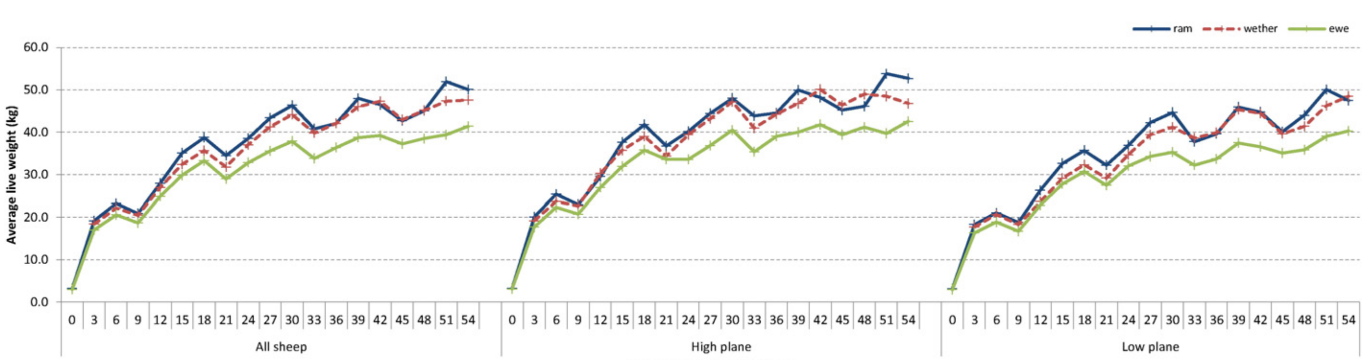

Fig. 5. Live weight data for different sexes (mean values). From an initial sample of 88 rams, 88 wethers and 156 ewes in the combined flock, sample size at each weigh-in decreases following biannual slaughters (see Table 1 for total sample size at each observation and supplementary data Table A3, live data, for sample size by sex following first slaughter at 7 months).

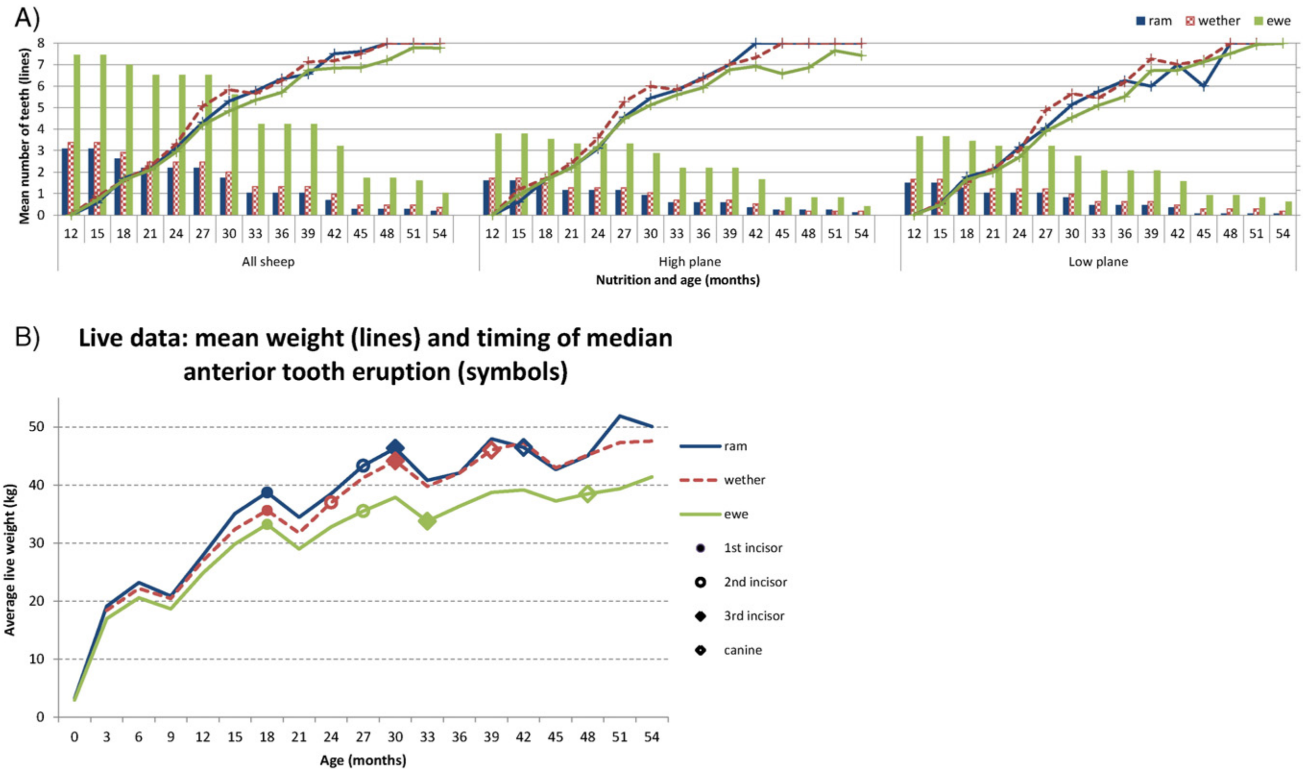

Fig. 6. Live tooth eruption data by sex, A) mean number of teeth; B) timing of median anterior tooth eruption ages against mean weight (combined flocks).

Whilst small, the influence of sex appears to be greater than that of nutrition (Section 4.2.2, Fig. 2), and greatest in later erupting anterior teeth (from 27 months).

Turning to skeletal anterior tooth eruption data, slight variation is evident from cohort 3 (i.e., slightly later than the 18 month live data observation), but with no consistency in ranking by sex and no variation is statistically significant (supplementary data Table A4; only samples with more than five sheep of each sex were tested).

Breeding and breeding age appear to have no impact on anterior tooth eruption in ewes from live data (Fig. 7), however skeletal data reveal some significant differences. Comparing unbred and bred ewes (early & late), only the combined nutrition flock in cohort 6 shows significant variation, with the median score higher for bred sheep (Fig. 8, supplementary data Table A5). Barren, unsuccessful pregnancy and twin-bearing ewes have not been excluded from these analyses.

4.3.3. Sex and management and cheek tooth eruption and wear

Skeletal cheek tooth data show very similar distributions of M2 and M3 eruption stages between sexes. Kruskal–Wallis tests confirm that no significant differences are seen between sexes within each nutritional flock or irrespective of nutrition (supplementary data Table A4). The effect of breeding cannot be examined in cheek tooth eruption data, as the M2 and M3 erupt prior to the age of first breeding.

The range of cheek tooth wear stages seen in rams, wethers and ewes overlaps within all tooth-cohorts. However, it is evident that sex does affect tooth wear, with variation in median values of up to three stages seen in 29 of 36 tooth-cohort-nutrition groups tested (supplementary data Table A6), and statistically significant variation found in ten groups, almost all older cohorts (Table 4A). From cohort 4&5 the

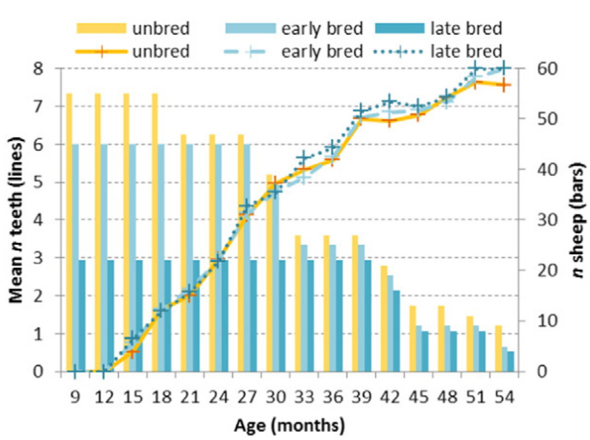

Fig. 7. Ewe live data for mean anterior tooth eruption by breeding status. The early and late bred ewes first lambed at 24 months and 36 months respectively.

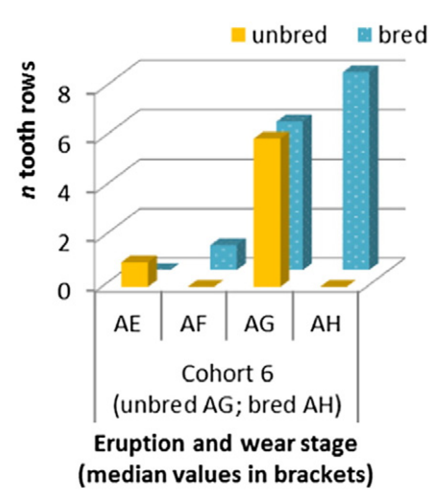

Fig. 8. Ewe skeletal anterior tooth row eruption and wear data, for cohort showing significant variation by breeding age. See Fig. 3 for stage definitions.

Table 4
Summary of Kruskal–Wallis test significant differences (p values) in wear between sexes irrespective of and within nutrition groups. Full results in supplementary data Tables A6 and A7.

Tooth	Cohort	A) Comparing ram, wether and combined ewes			B) Comparing ram, wether and ewe breeding groups[a]		
		All	High	Low	All	High	Low
M1	1	–	0.048	–	n/a	n/a	n/a
dp4	2&3	–	–	–	n/a	n/a	n/a
M2	2&3	–	–	–	n/a	n/a	n/a
P4	4&5	–	–	–	–	–	–
M2	4&5	–	–	–	–	–	–
M3	4&5	–	–	0.012	–	–	0.028
P4	6&7	–	–	0.043	–	–	–
M1	6&7	0.037	–	–	–	–	–
M3	6&7	0.021	–	–	–	–	–
P4	8&9	0.012	–	0.031	0.030	–	–
M1	8&9	<0.000	0.044	0.003	0.001	–	0.012
M3	8&9	–	–	–	–	–	–

[a] Barren and twin bearing sheep have not been excluded from their breeding groups in this analysis.

sample sizes of rams, wethers and ewes become more uneven as groups of bred ewes are introduced into the dataset (Table 2). Dividing the dataset into sex and breeding groups reduces the number of significant differences to four groups (Table 4B, supplementary data Table A7).

In most groups, including all statistically significant tooth-cohorts, rams show the highest, or joint highest, median wear scores (Fig. 9, supplementary data Table A6). Overall, our data suggest an age related trend in the ranking of median cheek tooth wear scores between wethers and ewes, although variation has only been shown to be significant in some cases.

Combining the sheep from both nutritional planes, in younger cohorts (up to 4&5) wethers always rank equally worn or less worn than ewes, with the reverse seen in older cohorts (6&7 and 8&9) (Fig. 9A). If ewe breeding groups are also considered, in cohort 4&5 only bred ewes exceed wethers, and in older cohorts, median wether wear is equal to or greater than the wear seen in each ewe breeding group (Fig. 9B, supplementary data Table A7). This trend is not observed in skeletal anterior tooth eruption data (Section 4.3.2).

The number of significant differences between sexes and between sexes and breeding groups is influenced by nutrition, with high plane sheep showing fewer than low plane sheep (Table 4, supplementary data Tables A6 and A7). First molar wear in cohort 8&9 is the tooth that most frequently exhibits variation at 99%, and is the only tooth-cohort to show significant variation by sex in the combined flock and within each nutritional plane.

The trends in ranking by sex and in sex-breeding group are only slightly less clear within each nutritional regime, than in the combined nutrition flocks. In a minority of tooth-cohorts, rams are no longer always positioned amongst the most worn, but the age related pattern of wether and ewe breeding group median wear rank generally persists (Fig. 9C–F).

Within the ewes, age of first breeding has very little impact and no consistency in the direction of any variation in median wear score. There are no significant differences within the combined plane flock or within each nutritional plane (supplementary data Tables A8–A9). Barren and twin bearing ewes have not been excluded from the dataset.

5. Discussion and conclusion

A collection of 356 Shetland sheep of known life history have provided a reference dataset for the eruption of incisors and canines through tri-monthly live observation, and from skeletal material at nine age cohorts. They have also provided a skeletal dataset for the eruption and wear of fourth premolar to third molar mandibular cheek teeth in the same age cohorts. The impact of this dataset on age at death estimation is considered elsewhere (Worley et al., in preparation). The influence of differing diet, sex, breeding age in ewes and castration of rams is reflected in the dental data, although often not to a statistically significant degree. This finding is important for zooarchaeological interpretation as it highlights that these variables should be of limited concern when comparing dental datasets, particularly where husbandry parameters (nutrition, environment) and sheep characteristics (hardiness, rate of maturation) are likely to have been similar to those of the experimental flock. Furthermore, the range of medium wear scores between sexes and paucity of significant variation in the dental data, support further investigation into comparison of dental and fusion data as a method for flock structure interpretation.

5.1. The impact of nutrition

The differing nutritional regimes were sufficiently varied to impact on weight gain (Section 4.2.1) with sheep receiving a native grassland diet achieving on average 10% lower body mass than those fed on improved grassland. The difference was also reflected in the size and shape of longbones, particularly in ewes (Section 2.2.2.1), and in the timing and duration of longbone fusion (Section 2.2.2.2), with the high plane animals reaching skeletal maturity earlier than those in the low plane group. Low quality nutrition can be seen to impact on dental maturity, with eruption of incisors seen earlier in high than low plane live data, and in the median scores of significantly varied skeletal data. Our data therefore support the general conclusions of other studies (Arrowsmith et al., 1974; Gunn, 1967; Purser et al., 1982; Wiener and Purser, 1957) that sheep fed on improved pasture may exhibit earlier anterior tooth eruption than those fed on poor pasture. However, many cohorts show no significant variation and the ranges seen in high and low nutrition anterior tooth eruption counts (live data) and scores (skeletal data) heavily overlap. While our data support the assertion that poor quality of nutrition may retard anterior tooth eruption, the scale of influence appears small.

There are no significant differences in the cheek tooth eruption data, although eruption was only captured within our age cohorts for the second molars, third molars and a small number of fourth premolars, suggesting that the influence of nutrition on the eruption of teeth used in zooarchaeological age at death estimation is very limited.

The nutritional regimes impacted on tooth wear, with significant differences primarily seen in teeth exhibiting early wear. Where significant differences were identified, the median wear stage indicates that slightly less wear occurred in low plane nutrition flocks, although the range of wear shows considerable overlap between nutritional planes. The potential relationship between nutrition and tooth wear is complex. Our data strongly suggest that early eruption is unlikely to be solely responsible for increased wear in high plane sheep as those in younger cohorts show no early eruption of the M3. We also see significant impact of nutrition on ewes and wethers, but not rams, suggesting that the former are either more sensitive to nutrition, or some other variable is influencing their wear, perhaps adaptation of behaviour mitigating impact of poorer nutrition, or variation in exploitation of pasture (through choice or restricted access). Nevertheless, others have also recorded different impact of nutrition between sexes (for example, Field et al., 1990).

The Pentland Hills native grassland fields (low plane nutrition) are likely to be equivalent to poor acid pasture nationwide in the UK, and the improved pasture is likely to be similarly representative. We might expect spatial variation in the number of grass growing days, and therefore condition of the grassland dependant on temperature and rainfall (Grigg, 1995, 31–35). The difference in quality of forage was limited for welfare concerns by moving low plane sheep to better pasture when too severe weight loss occurred, with supplemental hay during snow cover, and by maintaining acceptable stocking levels. In general the nutritional quality of forage available to archaeological flocks in the UK is likely to be similar to that represented in the experimental conditions. Like other Scottish island and hill sheep, the Shetland

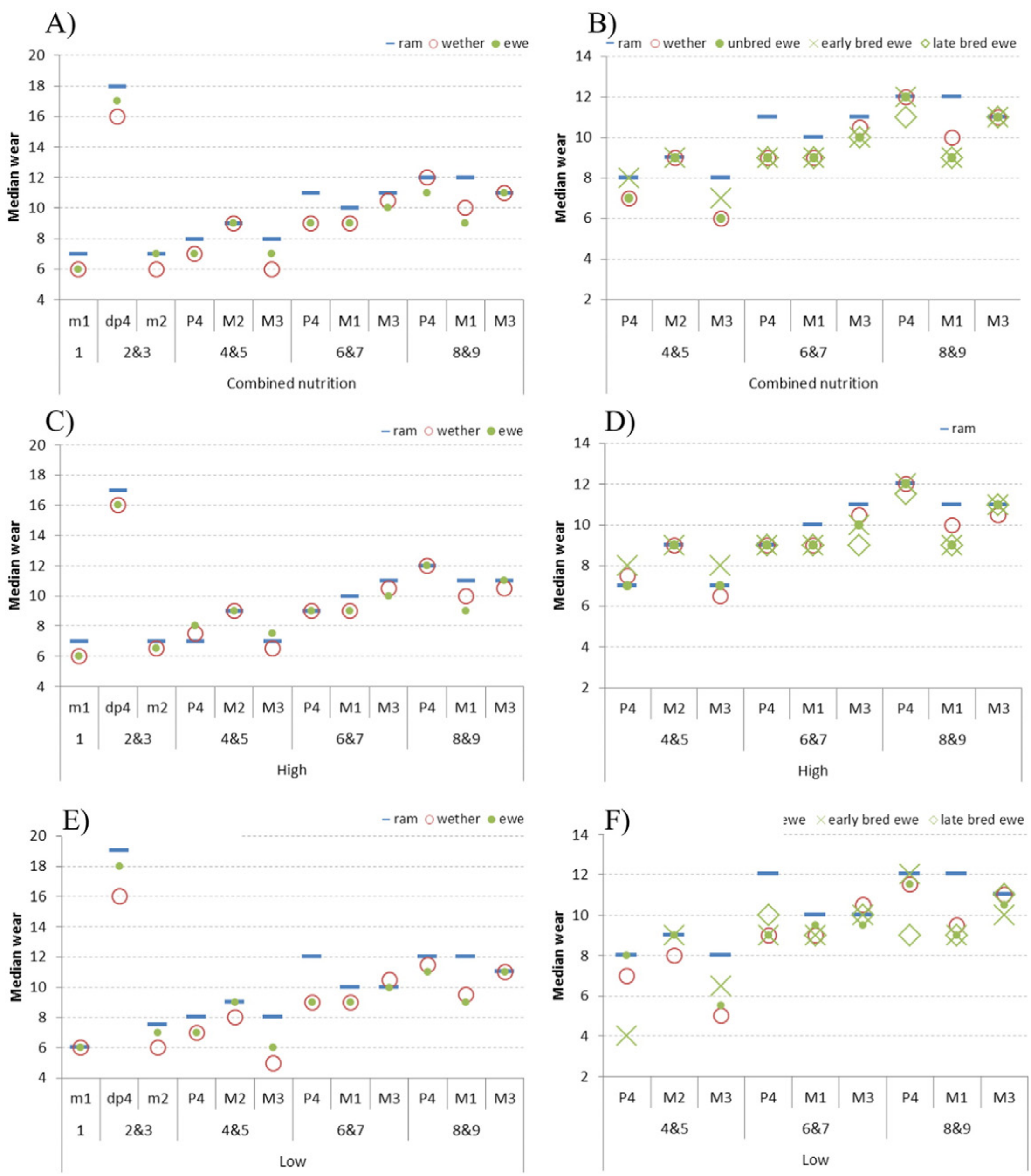

Fig. 9. Median tooth wear scores by sex (A, C, E) and sex and breeding ewe group (B, D, F). Table 4 identifies significantly varied results.

breed is renowned for hardiness (e.g., Allan, 1984). The impact of low quality nutrition on less hardy breeds, or of extreme malnutrition, might be a greater restriction of growth, and retardation of bone fusion and tooth eruption or wear in comparison with sheep fed on improved grassland. However, the degree of difference seen in our sheep suggests that variation in nutrition should be of minimal concern for comparative zooarchaeological analyses of UK assemblages.

5.2. The impact of sex, castration and breeding

The ewes are smaller (Section 2.1.2.1), achieve lighter average body mass at all weigh-ins, reach relatively stable adult weight earlier, and suffer less severe annual weight loss at older ages than the rams and wethers (Section 4.3.1). We note that there is some concordance between annual weight fluctuation and anterior tooth eruption, supporting previous assertions (McGregor, 2011), although rams which are consistently the heaviest sheep (mean weight), do not always show the most advanced anterior tooth eruption (mean or median live observation data).

Our data have shown that dental maturity is not impacted by sex in the same manner as skeletal maturity; while some ewe long bones fuse earlier than ram or especially wether bones (Section 2.1.2.2), ewe teeth erupt at around the same time or slightly later than those of male sheep. The live data show no difference in the first incisor, but the second and particularly third incisor and canine erupt later in ewes than males, and the second incisor and canine erupt later in rams than wethers. The skeletal data show slight differences in the median eruption of some teeth, but none are significantly varied. Our data therefore agree with some studies that wethers complete anterior tooth eruption (second incisor or canine) earlier than rams (Clutton-Brock et al., 1990; Hatting, 1983), and that there is no sexual distinction in the age of first incisor eruption (Matika et al., 1992), in contrast to data presented elsewhere

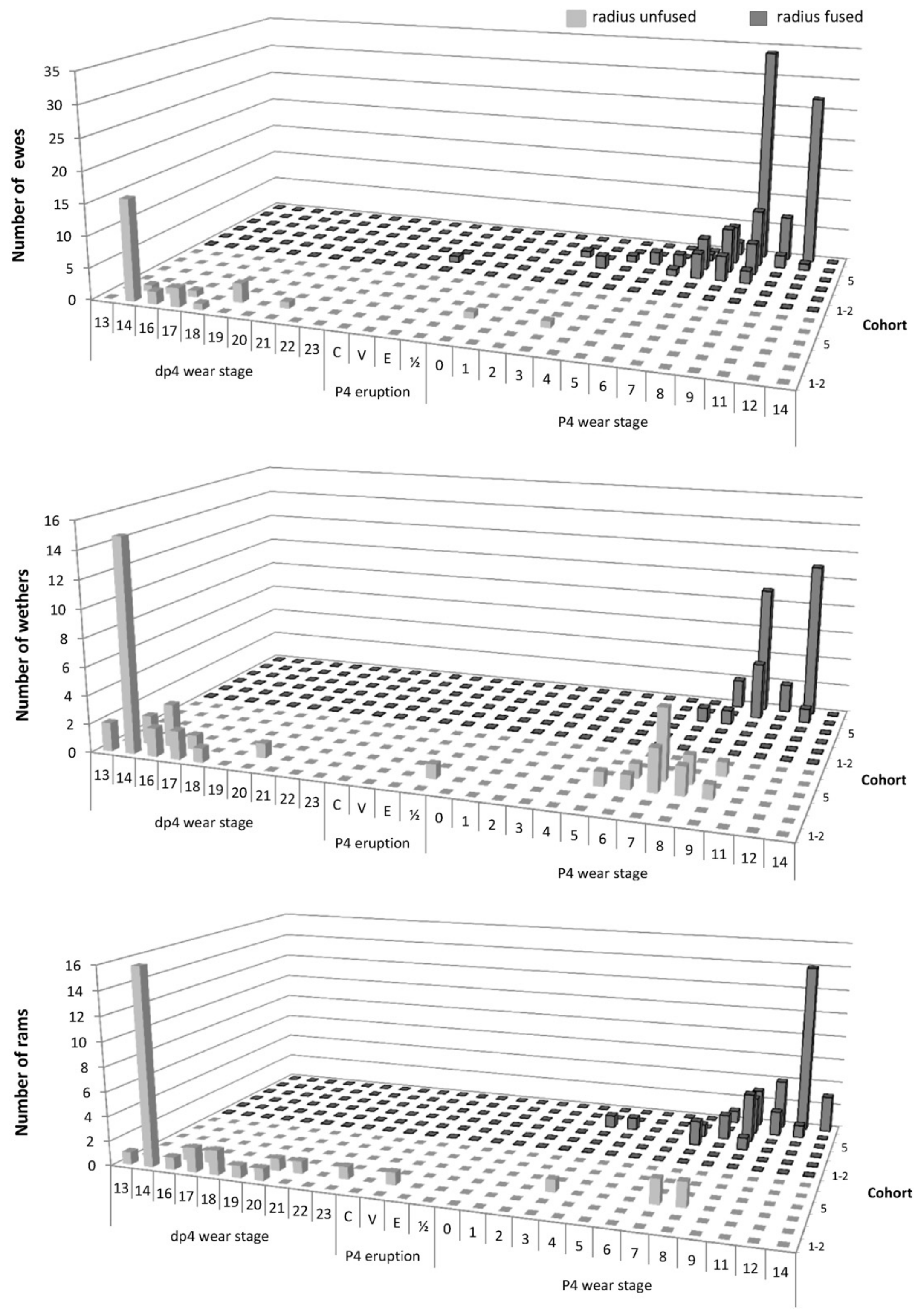

Fig. 10. Fusion of distal radius relative to fourth premolar tooth wear by cohort (1–9). Cohorts 1 and 2 and cohorts 7 to 9 are combined, as there is no variation in distal radius fusion and presence of dp4 or P4.

(Field et al., 1990; Table 4, Ho et al., 1989, Table 1). Ho et al.'s (1989) data highlight that the same degree of sexual variation cannot always be expected across breeds, particularly when comparing unimproved and improved modern sheep. Our data agree with Davis (2000) in showing that castration has little effect on cheek tooth eruption, in contrast to Clutton-Brock et al.'s (1990) conclusion that wether cheek teeth erupt relatively early.

While sex has little impact on eruption, it does impact on tooth wear. Significant differences are seen primarily in older cohorts (6&7, 8&9); their absence in younger cohorts exhibiting sensitive short-lived wear stages, suggests that the increasing divergence of tooth wear between sexes is associated with age rather than resolution of data (Section 4.1). For example, no fourth premolar cohorts show significant variation by sex until cohort 6&7 for low plane sheep or 8&9 for the combined flock and low plane; the M1 in the combined nutrition flock shows no significant variation in cohort 1, which includes only short lived wear stages, while cohorts 6&7 and 8&9, in which approximately 30% to 50% of teeth have progressed beyond the longstanding wear stages do show significant variation. Our data therefore support both Davis' hypothesis that variation in wear between sexes is greater in older sheep (Davis, 2000, 380) and also Jones (2006) findings of no sexual variation in wear in young sheep.

Median values suggest that where varied, ram wear is usually greater than that of wethers and ewes (in the combined nutrition flocks), and that relative wear of wethers and ewes varies with age. Our data therefore support the conclusions of Davis (2000) regarding relative ram and wether wear. We hypothesize that greater weight gain throughout life and more distinct seasonal weight gain seen in male sheep reflects differences in eating behavior that also result in cumulative variation in tooth wear by sex, with greater median tooth wear in rams.

While sex is seen to impact on dental data, the scale of the difference between the sexes is small, even in the oldest cohorts, and we therefore suggest that sexual variation is of limited concern for zooarchaeological comparative analyses, particularly in the comparison of populations of younger sheep (see Worley et al., in preparation).

Pregnancy and nursing might be expected to encourage feeding and therefore be reflected in increased tooth wear. Greater wear was observed in early bred compared to unbred ewes in cohort 4&5, but the difference is not significant and the pattern did not persist in older cohorts.

5.3. Comparison of variation/delay in dental evidence with that seen in fusion

The correlation of epiphyseal fusion and tooth eruption has been proposed as a tool for identifying management in archaeological sheep flocks. O'Connor (1982) and Payne (1988) compared the proportion of unfused bones in contemporaneous fusion points to the eruption and wear in mandibular tooth rows (O'Connor, 1982) or of isolated teeth (Payne, 1988, dp4/P4 ratio and M3 wear stage). Both authors speculated that a delay in fusion of the later fusing epiphyses relative to tooth/mandible age data might reflect the presence of wethers (O'Connor, 1982, 24; Payne, 1988, 108). Our study population supports this model, demonstrating marked sexual variation in fusion of later fusing epiphyses (Popkin et al., 2012) and little sexual variation in dental data. Consequently comparison of dental data corresponding to the period of sexual variation in fusion data remains a potential approach.

Here we compare radius distal fusion to eruption and wear of the fourth premolar. The radius distal epiphysis shows a considerable difference in age at fusion between ewes and wethers (Popkin et al., 2012) and potentially survives better in the archaeological record compared to other contemporaneous fusion points. Of all cheek teeth, the fourth premolar (dp4/P4) provides the greatest variety of tooth stages during the period of distal radius fusion (Fig. 10). Fusion occurs between P4 eruption stage V and wear stage 4 in ewes, between wear stages 3 and 9 in rams, and between wear stages 7 and 10 in wethers. The data therefore show that wethers, and to a lesser extent rams, have greater attrition relative to unfused late fusing epiphyses than ewes. The data for rams and wethers published by Davis (2000) conform to our trend, thus providing support for variation seen in this breed.

We also compared mandibular dentition (dp4/P4 ratio and M3 wear) to later fusing epiphyses following Payne's (1988) method for estimating sheep kill-off profiles. The results suggest a difference between dental and fusion data of 4% in ewes, 3% in rams and 15% in wethers. Assuming dental maturity is consistent (i.e., limited variation in eruption and wear) between sexes, fusion data slightly overestimate the proportion of older ewes, while the proportion of older males is underestimated, most markedly for wethers.

The paucity of dp4s in late wear and P4s in eruption or early wear impedes a clearer identification of sex variation with our current data. Forthcoming work will aim to fill gaps at these tooth stages (e.g., Baker et al., in preparation). The correlations of dental and fusion data may vary with breed; preliminary observation of other sheep breeds has shown some variation to the Shetland data. Zeder's (2006) data for Middle Eastern (mainly) wild sheep species show similar sexual variation, but with both ram and ewe fusion occurring at more advanced wear stages; this may reflect differences in environment and quality of forage, as well as genetic (wild vs domestic status) factors. Therefore, while the specific parameters identified for the Shetland sheep may only be applicable for similar geographical locations and environmental conditions, our data show that flock management can potentially be investigated through comparative analysis of dental and fusion data.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jasrep.2015.10.029.

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